Lubricating the swordfish head

Videler, John J.; Haydar, Deniz; Snoek, Roelant; Hoving, Henk-Jan T.; Szabo, Ben G.

Published in:
Journal of Experimental Biology

DOI:
10.1242/jeb.139634

© 2016. Published by The Company of Biologists Ltd | Journal of Experimental Biology (2016) 219, 1953-1956 doi:10.1242/jeb.139634

SHORT COMMUNICATION

Lubricating the swordfish head

John J. Videler[1,*], Deniz Haydar[2], Roelant Snoek[3], Henk-Jan T. Hoving[4] and Ben G. Szabo[5]

ABSTRACT

The swordfish is reputedly the fastest swimmer on Earth. The concave head and iconic sword are unique characteristics, but how they contribute to its speed is still unknown. Recent computed tomography scans revealed a poorly mineralised area near the base of the rostrum. Here we report, using magnetic resonance imaging and electron microscopy scanning, the discovery of a complex organ consisting of an oil-producing gland connected to capillaries that communicate with oil-excreting pores in the skin of the head. The capillary vessels transport oil to abundant tiny circular pores that are surrounded by denticles. The oil is distributed from the pores over the front part of the head. The oil inside the gland is identical to that found on the skin and is a mixture of methyl esters. We hypothesize that the oil layer, in combination with the denticles, creates a super-hydrophobic layer that reduces streamwise friction drag and increases swimming efficiency.

KEY WORDS: Swordfish, Functional morphology, Drag reduction, Oil gland, Porous skin

INTRODUCTION

Large predatory oceanic fishes show unique and extreme adaptations to hunt in the largest, yet least explored, habitat on the planet. These include omnidirectional camouflage (Brady et al., 2015), whole-body endothermy (Wegner et al., 2015) and extended rostrums (bills and swords) (Domenici et al., 2014). The swordfish (*Xiphias gladius* Linnaeus 1758; Xiphiidae) is probably the fastest swimmer on Earth. This species is intensively exploited but its behaviour remains virtually unknown because of the logistical difficulties associated with studying it in the pelagic realm. They are voracious but toothless predators feeding primarily on agile, fast-swimming pelagic squid (Hernandez-Garcia, 1995; Markaida and Hochberg, 2005). Swimming speeds of swordfish are estimated to reach values of well over 100 km h^{-1} (Barsukov, 1960). The swordfish is built for speed: the streamlined body (not including the sword) has a close to optimal thickness-to-length ratio of approximately 0.24, which offers the smallest pressure drag for the largest volume (Hertel, 1966). In addition, the caudal peduncle is dorsoventrally flattened with deep notches on the dorsal and ventral side, and is fitted with lateral keels reducing the drag of lateral movements. The crescent-shaped tail fin has a high aspect ratio (height squared divided by the surface area) of 4.3, a hallmark of an extremely fast swimmer (Videler, 1996; www.fao.org/fishery/species/2503/en).

In adults, the sword can reach 40–45% of the body length. Its surface structure is rough and porous. The roughness has been interpreted as a micro turbulence generator suppressing flow separation and reducing drag (Videler, 1995). A recent study using computed tomography scans and biomechanical analysis confirmed the suitability of the sword as a tool to slash prey, but also revealed a weak, poorly mineralised area near the base of the rostrum just in front of the eyes (Habegger et al., 2015). The results of this study made us aware of the significance of anatomical features in the same area we found between 1996 and 2007. We reanalysed these to study that weak area and to detect possible drag-reducing adaptations of the swordfish head. We found an oil-producing gland in this poorly mineralised area, and discovered that it connects to a system of capillary vessels that transport the oil to tiny pores, surrounded by denticles, in the skin of the swordfish head. We discuss these anatomical structures in the context of drag reduction.

MATERIALS AND METHODS

For our studies, we used two adult swordfish (approximately 1.6 m total length) that were acquired from commercial fishers and caught in the Mediterranean off the Corsican coast near Calvi in 1996. The fish were kept on ice on board the fishing vessel and were deep frozen directly after landing. Both specimens were kept frozen until examination. These specimens and two additional heads obtained from commercial fishers were used for dissections; one of the Corsican specimens was used for the magnetic resonance imaging (MRI) studies. The MRI examinations and the dissections were carried out in 1996 and 1997, when no national or international legislation regarding such studies on commercially available dead fish was in force.

The MRI apparatus used was a Siemens Magnetom Vision 1.5T System (field of view 25.6 mm, acquisition matrix 512×512, pixel size 0.5 mm; T1 weighted sequence, with a repetition time of 540 ms and an echo time of 12 ms, and a number of averages of 2).

The MRI studies comprised 657 pictures of sagittal and transverse sections of the entire body from the tip of the sword to the end of the tail. For our analysis, we used 25 sagittal sections (slice thickness 4 mm) of a 174-mm-long section of the head, starting at a position 48 cm from the tip of the sword. We also used 23 cross-sections (slice thickness 3 mm), covering the most anterior 66 mm of the 174 mm section (Figs S1–S3).

Standard dissection techniques and stereo microscopes were used to verify the attributes of anatomical details seen in the MRI pictures.

Skin surface topography was studied using stereo microscopes with magnifications of up to 50×, a transmission microscope with 500× magnification and scanning electron microscopy (SEM). The capillary vessel system in the skin was studied by observations of dissected slices of skin using back illumination. The distribution of

[1]Prof. Em. Groningen & Leiden University, Zuidlaarderweg 57, Noordlaren 9479 TH, The Netherlands. [2]Faculty of Behavioural and Social Sciences, University of Groningen, Grote Kruisstraat 2/1, Groningen 9712 TS, The Netherlands. [3]Waterproof, Marine Consultancy & Services BV, Flevo Marina Trade Centre, IJsselmeerdijk 2, Lelystad 8221 RC, The Netherlands. [4]GEOMAR Helmholtz Centre for Ocean Research Kiel, Düsternbrooker Weg 20, Kiel D-24105, Germany. [5]Faculty of Medical Sciences, Groningen University, Institute for Medical Education, Antonius Deusinglaan 1, Groningen 9713 AV, The Netherlands.

*Author for correspondence (j.j.videler@rug.nl)

J.J.V., 0000-0003-1226-9528

Received 29 February 2016; Accepted 17 April 2016

pores in the skin was determined by counting the number of pores per cm^2 surface area at 10 positions on the left side of the head, approximately evenly distributed from the base of the rostrum to the edge of the operculum. Connections between the pores and the capillaries were established by injecting Indian ink (diluted 1:1 with water or immersion oil) into the capillaries. Sizes and shapes of the pores were studied using SEM (JEOL JSM-6301 F, accelerating voltage 2 kV, lens aperture 30 µm). Skin samples were dehydrated in a graded ethanol series, air-dried and gold sputter-coated.

The oil properties were analysed using a gas chromatography flame ionisation detector (GC-FID, Shimadzu GC 17 with FID detector) and optimised by mass spectrometry (GC-MS, Agilent GC with MS detector). The HP5 column dimensions were 30 m×25 mm×0.25 µm in each experiment. Samples were taken from the oil inside the gland and from oil squeezed out of the skin of the head using a syringe.

To study the oil flow from the gland to the skin pores, the temperature of the oil gland was increased using a hair dryer. The warm airflow directed at the position of the gland induced oil excretion from the pores.

RESULTS AND DISCUSSION

The MRI scans reveal the presence of a large gland in the anterior part of the upper jaw immediately posterior to the origin of the rostrum. Its dorsal margin is ventral to the orbit (Fig. 1, Figs S1, S2). In a swordfish with a total length (TL) of 1.6 m, the total volume of the gland is approximately 46 cm^3, which is approximately 56% of the volume of the relevant section of the upper jaw. The cross-sectional area of the gland relative to that of the upper jaw reaches maximum values approaching 50% in cross-sections 8 and 9 (Fig. S2). The gland consists of three compartments: an anterior central part that widens into two lateral lobes posteriorly. The posterior side of the interconnected lateral lobes is dorsoventrally curved and covers the anterior margins of the orbit. Folded bony ingrowths from the ventral and lateral regions enlarge the surface area of the gland and are covered with an epithelium. Near the orbit, the gland is divided into a right and a left part. Dissection showed that all compartments were saturated with oil.

A network of capillary vessels in the skin is distributed over a large part of the head, from the origin of the sword up to the edges of the opercula (Fig. 2). The outermost sagittal MRI scan (Fig. 2A) shows one branch of that network in the skin posterior to the eye. This network is connected to the oil gland and is present in the concave anterior and lateral parts of the head (Fig. 2B). The diameter of the vessels varies between 0.05 and 0.1 mm. Wider main vessels run from the three main parts of the gland towards the areas dorsal and ventral to the eyes and to the skin covering the gland. Side vessels branch repeatedly and cross-connections between different branches occur (Fig. 2C). The vessels narrow down towards blind ends. Along the vessels, numerous round pores open to the exterior of the skin, varying in abundance between 4 and 25 pores cm^{-2} (Fig. 2D). The diameter of the pores varies between

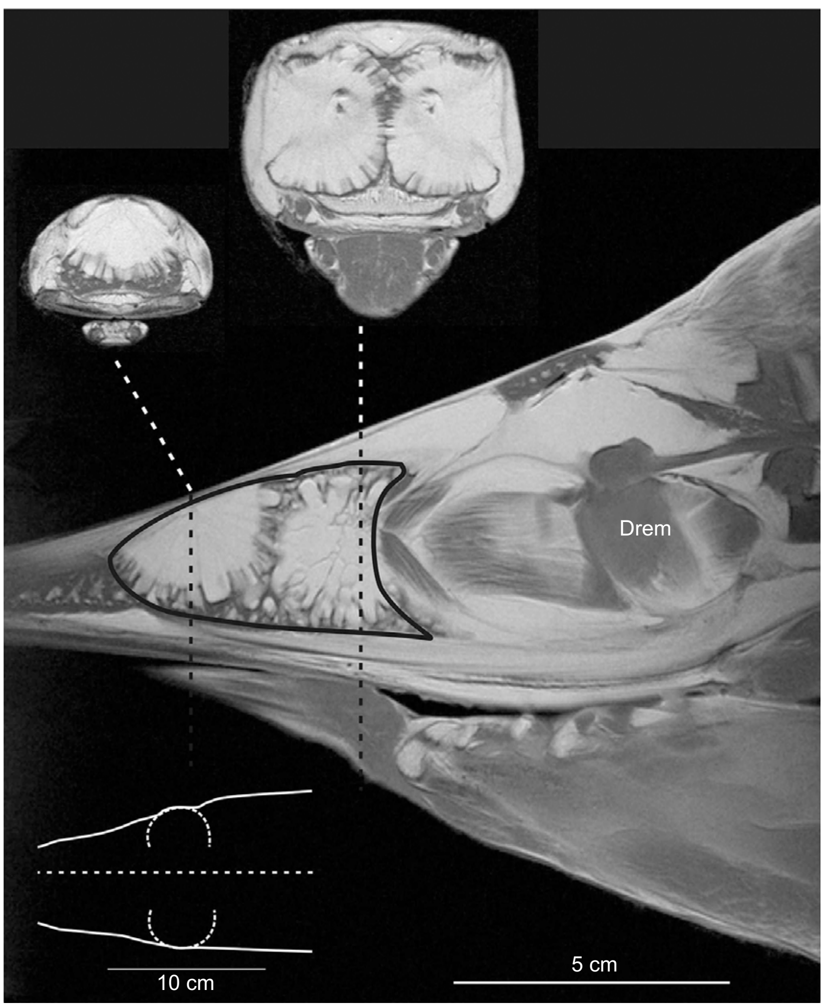

Fig. 1. The position of the oil gland in the swordfish head. The main picture is a sagittal MRI section approximately through the median plane. (The drawing in the lower left-hand corner gives the exact position as seen from the dorsal side, with eyes indicated by curved dashed lines.) The contour of the oil-producing gland is outlined in black. Two scans of cross-sections at positions indicated by the dashed lines show the anterior central part of the gland in the left cross-section and the two lateral lobes close to the eyes in the right cross-section. ‘Drem’ indicates the position of the heat-producing dorsal rectus eye muscle. The sagittal section is number 13 in Fig. S1. The anterior cross-section is number 9 in Fig. S2A and the posterior cross-section is number 21 in Fig. S2B.

Journal of Experimental Biology (2016) 219, 1953-1956 doi:10.1242/jeb.139634

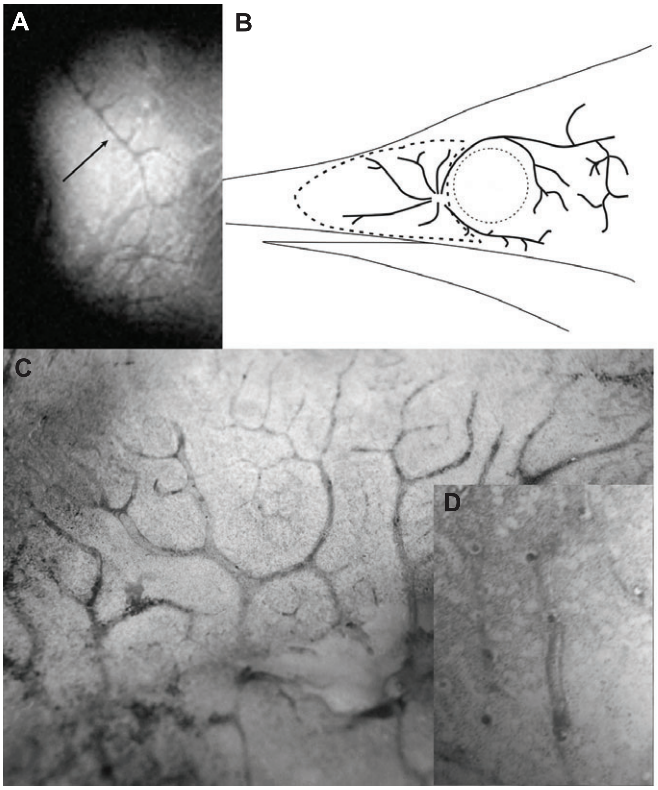

Fig. 2. The capillary network on the swordfish head. (A) MRI scan of the outermost sagittal section of the head. The arrow points to a fragment of the extended capillary network in the skin of the head just behind the eye. (B) A reconstruction based on careful dissection of the skin of the main afferent vessels of the capillary network originating from the oil gland. (C) Part of the skin of the operculum in back illumination, revealing the density of the network. (D) Detail of the network showing the pores connecting the vessels with the external environment.

0.05 and 0.28 mm. The highest pore densities occur near the edges of the opercula and in the region covering the oil gland. The pores are circular and surrounded by denticles (Fig. 3A). Single denticles that were not associated with pores (~15 per mm^2) (Fig. 3B) were also observed on the skin.

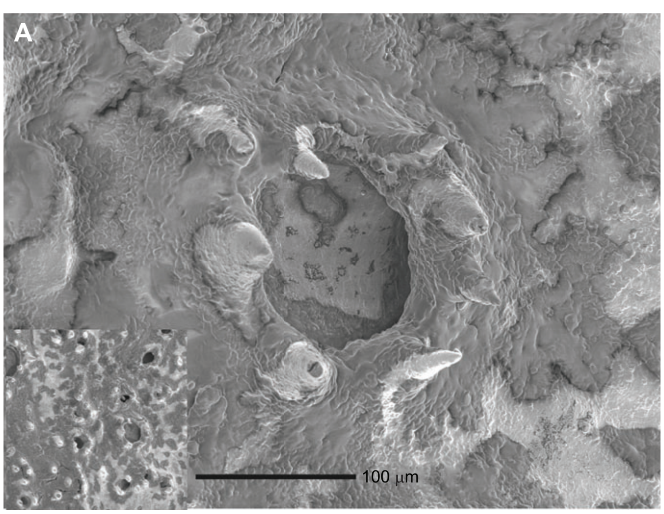

Fig. 3. Pores in the capillary network on the swordfish head. (A) Detail of a single pore. The pore diameter is ~0.1 mm and it is surrounded by seven denticles. (B) The inset shows a surface area of 1 mm^2 around the pore. The sample was taken from the skin between the eyes.

During dissection of the head, the oil was observed to flow out of the pores as soon as the oil gland was heated. The oil congealed at temperatures below 8°C. The chemical composition of oil sampled inside the gland and oil taken from the skin surface was identical. Mass spectrometric analysis revealed a mixture of methyl esters – fatty acids commonly found in plants and animals – consisting mainly of: palmitic acid ($C_{17}H_{34}O_2$, hexadecanoic acid m.e.; 25 µg mg^{-1}, 97.5 µmol g^{-1}), oleic acid ($C_{19}H_{36}O_2$, 9-octadecenoic acid m.e.; 24 µg mg^{-1}, 85 µmol g^{-1}), myristic acid ($C_{15}H_{30}O_2$, tetradecanoic acid m.e.; 5 µg mg^{-1}, 21.9 µmol g^{-1}) and stearic acid ($C_{19}H_{38}O_2$, octadecanoic acid m.e.; 4 µg mg^{-1}, 14.1 µmol g^{-1}).

The mechanism causing the oil to flow through the network of capillaries and to exude through the pores in the skin is not obvious from the anatomy. A possible explanation could be offered by the results of dynamic pressure measurements over the surface of a 65 cm TL wood model of a swordfish in a flow tank at 6 m s^{-1} flow speed (Aleyev, 1977). The dynamic pressure coefficient [defined as: $2(p–p_0)/\rho V^2$, where p is the pressure at the point of investigation, p_0 is the static pressure in the free stream, ρ is the water density and V is the velocity of the free stream of 6 m s^{-1}] along the dorsal side of the head drops from a maximum value (+0.13) near the base of the sword to a minimum (−0.39) at the dorsal fin (Fig. S3). The sub-ambient dynamic pressure over the front part of the head might suck oil out of the pores. It would also provide a functional explanation for the unique shape of the swordfish head.

This newly discovered lubricating organ thus consists of an oil-producing gland and a network of capillary vessels with pores to the outside. We propose glandula oleofera and rete lubricans, respectively, as scientific names for these structures.

Swordfish possess a heat-producing organ that uses a modified ventral part of the dorsal rectus eye muscle (Carey, 1982). Thermogenic cells inside the muscle enhance the local temperature (Block, 1986; De Metrio et al., 1997), and arterial blood is in countercurrent heat exchange with blood in the veins (Fig. 1). Heat transfer to the brain and eyes is mainly conductive (De Metrio et al., 1997). The eyes are heated and well insulated from the rest of the head. The rear part of the oil gland closely abuts the eye and increased temperatures can be expected to reach the oil gland. This may allow the oil to remain fluid and flow from the gland to the pores in the skin. The oil solidifies below approximately 8°C, making it persistent on the skin in cold seawater. In the Western North Atlantic, tagged swordfish were shown to hunt in deep water with temperatures down to 8°C during the day and characteristically occupy surface waters of less than 100 m during the night (Carey and Robison, 1981; Lerner et al., 2013).

The excreted oil on the skin of the head makes the skin surface hydrophobic, causing hydrodynamic slip by changing the boundary layer conditions. Slippery hydrophobic surfaces at the solid–water interface have a viscous drag-reducing effect in the streamwise direction in turbulent high-Reynolds-number flow (Choi et al., 2003; Min and Kim, 2004). Super-hydrophobic layers with rough microstructures have recently been shown to decrease frictional drag by more than 20% (Luo et al., 2015). The swordfish head surface meets the super-hydrophobic requirements: the oil provides a hydrophobic layer and the skin denticles provide the required roughness.

Swordfish cannot be kept in captivity, and their extreme swimming habits and mesopelagic way of life make measurements of the function of the lubricated skin in the field virtually impossible. However, modeling the swordfish features in fast water tunnels could test our hypothesis and offer new perspectives for biomimetics studies aimed at drag reduction.

The swordfish oil-gland system, with its capillary vessels, pores in the skin and the purported drag reduction, is the latest addition to the repertoire of unique adaptations that may enable swordfish to catch fast-swimming, very agile prey, and is an illustration of the evolutionary arms race in the open ocean between the fastest swimming predators and the fastest swimming prey.

Acknowledgements
We thank the University Medical Centre Groningen, the Netherlands, and the MRI team of the Department of Radiology for the unique opportunity to scan the swordfish during the wee hours without harming patients' interest. Theodora Tiemersma-Wegman and Jos de Wiljes are thankfully acknowledged for the chemical analysis of the oil. J. Stokroos of the laboratory for Cell Biology & Electron Microscopy took the SEM pictures of skin pores. Hanneke Videler critically read the manuscript. Tennie Videler's contribution to the editing and formatting process was invaluable.

Competing interests
The authors declare no competing or financial interests.

Author contributions
J.J.V. is the initiator of the swordfish project of the former department of Marine Biology of Groningen University. R.S. discovered the capillary network during his master's project. D.H. and H.-J.T.H. prepared and analysed SEM pictures of the pores in the skin. B.G.S. initialised and supervised the MRI procedure.

Funding
This research received no specific grant from any funding agency in the public, commercial or not-for-profit sectors.

Supplementary information
Supplementary information available online at
http://jeb.biologists.org/lookup/suppl/doi:10.1242/jeb.139634/-/DC1

References
Aleyev, Y. G. (1977). *Nekton*. The Hague: Junk.
Barsukov, V. V. (1960). The speed of movement of fishes. *Priroda* **3**, 103-104 (in Russian).
Block, B. A. (1986). Structure of the brain and eye heater tissue in marlins, sailfish, and spearfishes. *J. Morphol.* **190**, 169-189.
Brady, P. C., Gilerson, A. A., Kattawar, G. W., Sullivan, J. M., Twardowski, M. S., Dierssen, H. M., Gao, M., Travis, K., Etheredge, R. I., Tonizzo, A. et al. (2015). Open-ocean fish reveal an omnidirectional solution to camouflage in polarized environments. *Science* **350**, 965-969.
Carey, F. G. (1982). A brain heater in the swordfish. *Science* **216**, 1327-1329.
Carey, F. G. and Robison, B. H. (1981). Daily patterns in the activities of swordfish, *Xiphias gladius*, observed by acoustic telemetry. *Fish Bull.* **79**, 277-292.
Choi, C.-H., Westin, K. J. A. and Breuer, K. S. (2003). Apparent slip flows in hydrophilic and hydrophobic microchannels. *Phys. Fluids* **15**, 2897.
De Metrio, G., Ditrich, H. and Palmieri, G. (1997). Heat-producing organ of the swordfish (*Xiphias gladius*): a modified eye muscle. *J. Morphol.* **234**, 89-96.
Domenici, P., Wilson, A. D. M., Kurvers, R. H. J. M., Marras, S., Herbert-Read, J. E., Steffensen, J. F., Krause, S., Viblanc, P. E., Couillaud, P. and Krause, J. (2014). How sailfish use their bills to capture schooling prey. *Proc. R. Soc. B Biol. Sci.* **281**, 20140444.
Habegger, M. L., Dean, M. N., Dunlop, J. W. C., Mullins, G., Stokes, M., Huber, D. R., Winters, D. and Motta, P. J. (2015). Feeding in billfishes: inferring the role of the rostrum from a biomechanical standpoint. *J. Exp. Biol.* **218**, 824-836.
Hernandez-Garcia, V. (1995). The diet of the swordfish *Xiphias gladius* Linnaeus, 1758, in the central east Atlantic, with emphasis on the role of cephalopods. *Fish Bull.* **93**, 403-411.
Hertel, H. (1966). *Structure, Form and Movement*. New York: Reinhold.
Lerner, J. D., Kerstetter, D. W., Prince, E. D., Talaue-McManus, L., Orbesen, E. S., Mariano, A., Snodgrass, D. and Thomas, G. L. (2013). Swordfish vertical distribution and habitat use in relation to diel and lunar cycles in the Western North Atlantic. *Trans. Am. Fish. Soc.* **142**, 95-104.
Luo, Y., Wang, L., Green, L., Song, K., Wang, L. and Smith, R. (2015). Advances of drag-reducing surface technologies in turbulence based on boundary layer control. *J. Hydrodyn. B* **27**, 473-487.
Markaida, U. and Hochberg, F. G. (2005). Cephalopods in the diet of swordfish (*Xiphias gladius*) caught off the West Coast of Baja California, Mexico. *Pac. Sci.* **59**, 25-41.
Min, T. and Kim, J. (2004). Effects of hydrophobic surface on skin-friction drag. *Phys. Fluids* **16**, L55.
Videler, J. J. (1995). Body surface adaptations to boundary layer dynamics. In *Biological Fluid Dynamics* (ed. C. P. Ellington and T. J. Pedley), pp. 1-12. Cambridge: The Society of Biologists.
Videler, J. J. (1996). *Fish Swimming*. London: Chapman & Hall.
Wegner, N. C., Snodgrass, O. E., Dewar, H. and Hyde, J. R. (2015). Whole-body endothermy in a mesopelagic fish, the opah, *Lampris guttatus*. *Science* **348**, 786-789.